

Population Responses of *Microtus pennsylvanicus* across a Chronological Sequence of Habitat Alteration¹

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ABSTRACT. Understanding the effects of habitat alteration on population demography and persistence is emerging as one of the most important and challenging areas facing ecologists and conservation biologists today. Here we compare the population demography of a common but important consumer species in eastern and mid-western grassland communities (*Microtus pennsylvanicus*) across three habitats that differ in the amount of time since reclamation following strip-mining (30, 25, and 15 years). We established two 40 × 40 m plots at each of the three sites and used traditional capture-recapture techniques to monitor population size, survival, and recruitment through a nine-month period during 1999-2000. We predicted that populations of *M. pennsylvanicus* would exhibit higher population numbers, better survival rates, and higher rates of recruitment in habitat patches that had been recovering for longer periods of time. In contrast to our predictions, results indicated higher peak population numbers at the most recently disturbed site ($\bar{x} = 81.18 \pm 9.59$ individuals) and higher numbers of reproductive females ($\bar{x} = 3.38 \pm 0.85$) relative to sites recovering for 25 and 30 years (\bar{x} peak population size = 28.08 ± 23.09 and 31.16 ± 1.75 individuals, respectively; \bar{x} number of reproductive females = 0.57 ± 0.32 and 1.13 ± 0.13 , respectively). Thus it would appear that time since disturbance was not an important predictor of population performance for this species in this altered system. Alternative hypotheses such as the influence of local habitat attributes and population fluctuations are discussed.

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INTRODUCTION

In the eastern United States, surface mining for Appalachian coal has yielded vast landscapes of severely altered habitat (Carter and Ungar 2002). Since 1972 surface mining operators in the state of Ohio have been required to engage in prescribed reclamation efforts that include restoration of top soil and high-density broadcast seeding of grasses and trees (Arnold, Ohio DNR, personal communication). While reclaimed areas can provide important living and breeding habitat for a variety of species (particularly those oriented to open grassland habitat), it is unclear whether such habitats will ultimately return to states resembling pre-disturbance conditions or support pre-disturbance levels of species diversity and ecosystem function.

A number of investigations have been conducted looking at the effects of surface mining on plant ecology (Bell and Ungar 1981; Holl and Cairns 1994; Carter and Ungar 2002). There have also been a number of studies focused on avian and lepidopteran consumer species (Holl 1996; Bajema and Lima 2001; Ingold 2002). There has, however, been very little published on the ecology of small mammals in post-mining, reclaimed habitats. That such a gap exists in the literature seems surprising. Indeed, there are a number of reasons to suspect that an understanding of how small mammals influence patterns of ecosystem recovery might prove important. First, herbivory by small mammals can significantly alter patterns of succession and plant community development (Bowers 1993; Howe and Brown 1999). In addition, small mammals play important roles in ecosystems by providing food for a wide variety of avian, reptilian, and larger mammalian predators (Golley and others

1975). Finally, the depth and complexity of small mammal communities provide important indicators that reflect the growth, development, and maturation of ecosystems (French and others 1968). Thus, examining the distribution, diversity, and demography of small mammal communities is likely an important key to understanding the nature and trajectory of ecosystem recovery in reclaimed habitats.

Objective

Our objective for this research was to compare the population performance of meadow voles (*Microtus pennsylvanicus*) across grassland habitats that constitute a gradient in the amount of time since reclamation. Given there has been little previous analysis of small mammal demography across sites in different stages of recovery from surface mining, our naive expectation was that population performance (as reflected in population size and demography) would be positively related to the amount of time since mining occurred. Our objective for this research then was to address the following question:

Is population performance of *Microtus pennsylvanicus* positively related to the amount of time since disturbance in habitats that are recovering from surface-mining?

In order to address this question we compared population performance of *Microtus pennsylvanicus* and local habitat features across study sites that have been recovering from surface mining for approximately 30, 25, and 15 years, respectively.

MATERIALS AND METHODS

Study Site

The Wilds (International Center for the Preservation of Wild Animals) is a major center for conservation

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research and education located on 3,700 hectares of land that has been surfaced mined twice in the last century. Formally owned by the Ohio Power Company, the most recent mining began in 1969 and proceeded north to south over the course of the next 15 years. Reclamation efforts began each year as soon as mining was completed, with the last reclamation work being completed in 1985 (Arnold, Ohio DNR; personal communication). Seeding generally included a heavy (58.5 kg/ha) inoculation with the following major constituents: rye grass (*Lolium* spp.; ca. 23%), orchard grass (*Dactylis glomerata*; ca. 14%), fescue (*Festuca* spp.; ca. 14%), Lespedeza (*Lespedeza cuneata*; 8%), alfalfa (*Medicago sativa*; ca. 7%), red clover (*Trifolium pratense*; ca. 7%), and redbud (*Agrostis gigantea*; ca. 6%).

Today, the reclamation zone is dominated by grassland habitat; little forest has reestablished across any of the areas that were mined. In addition, moving from north to south, there are clear differences in the density, species diversity, and structural complexity of grassland vegetation. In addition to our target species, other common consumer species include: short-tailed shrews (*Sorex cinereus*), native mice (*Peromyscus* spp.), bobolinks (*Dolichonyx oryzivorus*), Henslow's sparrows (*Ammodramus henslowii*), grasshopper sparrows (*Ammodramus savannarum*), and eastern meadowlarks (*Sturnella magna*). For our work we choose to focus on meadow voles (*Microtus pennsylvanicus*), one of the most common mammals found in the grassland habitats that predominate in many post-reclamation areas of the eastern United States. *Microtus pennsylvanicus* has been the subject of a great many ecologically oriented studies because: 1) populations often exhibit high enough numbers to allow for robust demographic estimation, 2) animals are easily handled, and 3) capture-recapture protocols have been well established (Dooley and Bowers 1998).

Field Methods

Study sites were established during April 1999 in the northern, central, and southern sections of the Wilds' property on sites that had been in recovery from surface mining for 30, 25, and 15 years (respectively). At each study site, two 40 × 40 m small mammal live trapping grids were established using Sherman live traps distributed in a 5 × 5 pattern with 10 m inter-trap station distances. Once established the study sites were trapped nine times (trap sessions ranged in duration from 2-5 nights) beginning in August 1999 and continuing until early April 2000 in order to provide capture/recapture data that could be used to estimate population size and other important demographic statistics (in particular: survival, recruitment, age distribution) for cross-site comparisons (Nichols 1992). Traps were baited in the early evening with peanut butter wrapped in wax paper, checked at first light, and were closed throughout the day. Animals captured for the first time were marked by toe clipping. For the first and all subsequent captures of each individual we recorded toe number, trap location, species, sex, reproductive condition, and body mass. Traps were locked open between monthly trap sessions

to allow free exploration and aeration.

Vegetation analysis was conducted twice: during March and September 1999. Random point vegetation measurements were taken at ten points in each plot using stem contact techniques as described in Dooley and Bowers (1996, 1998). At each point, the number of vegetative contacts of all species present was recorded at 0.1, 0.25, 0.5, and 0.75 m. In addition, four random thatch depth measurements (cm) were recorded for each point.

Analyses

Estimates of population size, demographic statistics, and capture probabilities for small mammals were developed using program JOLLY (version 01-24-91, provided by James E. Hines, National Biologic Service). For all plots except one (plot 6, located in the southern study site) we used model "D" within the JOLLY package that yields relatively precise estimates of demographic statistics as well as tool parameters such as capture probability with the trade-off of yielding only a single estimate of survival and capture probability instead of one estimate for each trap week. The demographic statistics estimated were survival (the probability of surviving from one trap session to the next) and recruitment (the number of individuals added to the population through both local births and immigration between trap sessions). For plot 6 this model did not produce an adequate fit to the data and therefore we selected a more generalized model with the trade-off that we were only able to estimate abundance for 8 instead of 9 weeks. Therefore, abundance for the southern study site during week 9 is represented by the estimate for plot 5 only instead of a mean for plots 5 and 6. Both small mammal population estimates and vegetation data were compared across sites using fixed-effects analysis of variance (ANOVA). Repeated measures models were used for all temporally based comparisons. Means are reported with \pm standard errors.

RESULTS

We recorded 507 captures (180 male, 326 female, 1 unknown) of 196 individual (83 males, 112 females, 1 unknown) *Microtus pennsylvanicus* in 11 trap sessions between June 1999 and April 2000. Both the mean number of captures as well as the mean number of individuals observed across the study period were higher at the southern site ($\bar{x} = 121.5 \pm 0.5$ and 55.5 ± 1.5 , respectively) relative to the central and northern sites ($\bar{x} = 76.0 \pm 9.0$ and 25.0 ± 3.0 ; 56.0 ± 22.0 and 17.0 ± 5.0 , respectively). By contrast, the mean number of juveniles observed across the study period (an indirect indicator of reproductive success) was highest at the central site ($\bar{x} = 15.5 \pm 4.5$) followed by the southern ($\bar{x} = 10.5 \pm 2.5$) and northern sites ($\bar{x} = 4.5 \pm 1.5$). Looking across all study sites, captures were generally low through June of 1999 and peaked in late August of that year (Fig. 1). Following a population decline through the winter of 1999-2000 (which is typical for this species) the number of captures began to rebound in April of 2000 at the end of the study. Capture probabilities across the study period were highest at the central site ($\bar{x} = 0.52 \pm 0.17$)

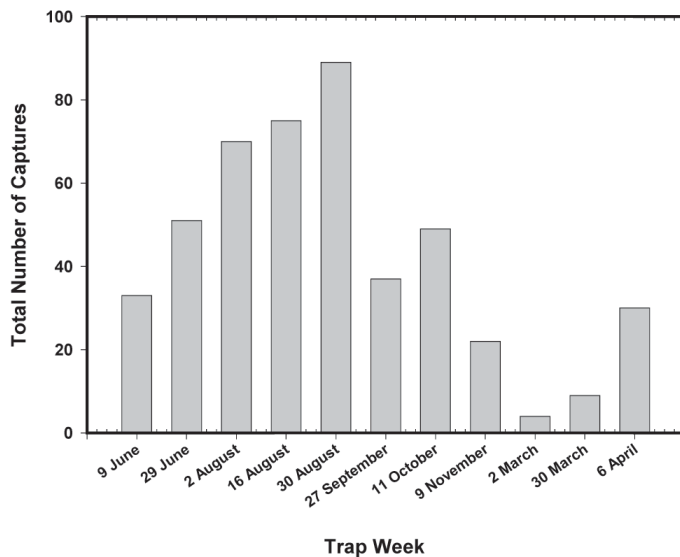


FIGURE 1. Total number of meadow vole (*Microtus pennsylvanicus*) captures across northern, central, and southern study sites at the Wilds 1999-2000.

followed by the northern ($\bar{x} = 0.25 \pm 0.04$) and southern sites ($\bar{x} = 0.24 \pm 0.07$). Site fidelity, as reflected in the ratio of the mean number of previously marked individuals observed across trap sessions to the mean estimated population size ranged from 0.36 at the central study site to 0.40 at the northern and 0.43 at the southern sites, respectively.

Population Size

Visual inspection of population size data for *M. pennsylvanicus* suggests population size was generally larger at the southern site than the central or northern sites (Fig. 2), however there was only a marginal statistical difference across all sampling periods ($F = 5.0$, $d.f. = 2$, $p < 0.12$). Clearly the most pronounced differences in population size between the southern and the other sites occurred during the summer sampling periods (8/02, 8/16, and 8/30). Indeed, mean population size rose to a peak of 81.18 ± 9.59 individuals at the southern site, but only 28.08 ± 23.09 and 31.16 ± 1.75 individuals at the central and northern sites, respectively. Limiting statistical comparisons to this period again suggests a stronger but still statistically marginal difference ($F = 6.9$, $d.f. = 2$, $p < 0.08$), however a *post-hoc* comparison indicated that there was a significant difference in mean population size between southern and central sites (Duncan *post-hoc* comparison, $p < 0.05$). After the 16 August trap session however, population size at the southern site began to decline to a point where it was relatively similar to what was observed at the central and northern sites. Estimated population size at all three sites remained low throughout the winter (generally < 10 individuals). Interestingly, at the start of the next growing season, population size at plot 5 (the one southern site plot that could be used for abundance estimation for that time period) again looked to be increasing at a greater rate than that observed at the central and northern sites (raw captures at plot 6, the other

southern plot, were also well above those observed at the central and northern sites).

Survival

Microtus pennsylvanicus populations at all three study sites exhibited reasonably high mean inter-trap session survival probabilities ranging from 0.70 at the central site to 0.77 and 0.88 at the southern and northern sites, respectively. Standard errors were reasonably small (ranging from 0.003 to 0.05), yet no statistically significant difference was detected for mean inter-trap session survival between sites ($F = 0.44$, $d.f. = 2$, $p > 0.67$).

Recruitment

Mean recruitment (the number of new individuals added to a population through local birth and immigration) was quite variable through time at all three sites (Fig. 3). Indeed, it appears that there was much more within-site variation than between-site variation. Perhaps as result, there was no evidence to suggest significant differences in mean recruitment between study sites ($F = 0.44$, $d.f. = 2$, $p > 0.67$). Still it is interesting to note that both mean and peak recruitment were highest at the southern site ($\bar{x} = 4.55$ and 19.33 individuals, respectively) relative to the central ($\bar{x} = 4.04$ and 15.5 individuals, respectively) and northern sites ($\bar{x} = 3.97$ and 13.83 individuals, respectively). Although it is difficult to accurately estimate differences in local reproduction as a component of total recruitment, one proxy index—the mean number of reproductive females observed across study periods (that is, females that were either pregnant or lactating when captured)—was highest at the southern site ($\bar{x} = 3.38 \pm 0.85$) relative to the central ($\bar{x} = 0.57 \pm 0.32$) and northern sites ($\bar{x} = 1.13 \pm 0.13$), though again the statistical difference was marginal ($F = 7.54$, $d.f. = 2$, $p < 0.07$).

Vegetation Analysis

Results from random point vegetation analysis provided an important compliment to the small mammal

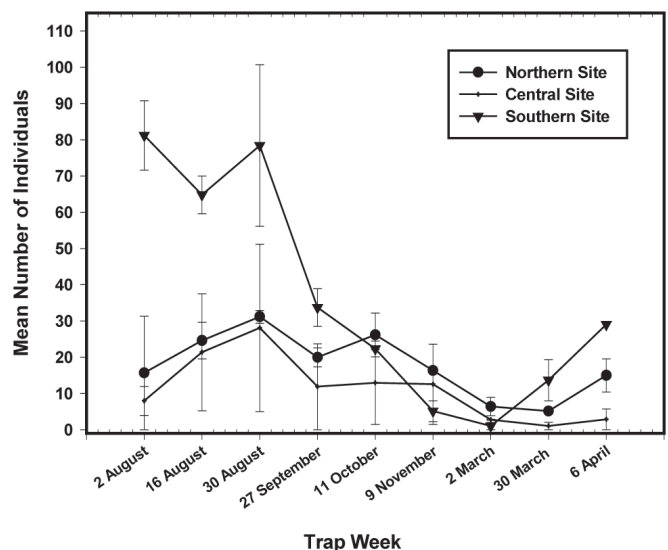


FIGURE 2. Meadow vole (*Microtus pennsylvanicus*) abundance across northern, central, and southern study sites at the Wilds 1999-2000.

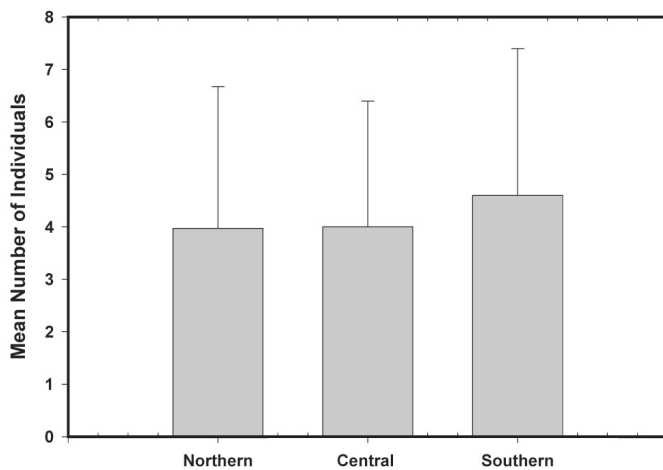


FIGURE 3. Meadow vole (*Microtus pennsylvanicus*) mean recruitment across northern, central, and southern study sites at the Wilds 1999–2000.

population analyses. Consistent with our expectations, the northern site exhibited greater structural diversity due in large measure to the presence of lespedeza (*Lespedeza cuneata*) and brome grasses (particularly smooth brome – *Bromus inermis*). Interestingly, the central site exhibited the greatest biotic diversity in grasses with four species observed. We observed two at the central site and one grass species at the northern and southern sites, respectively. However, from the standpoint of *M. pennsylvanicus*, the southern site probably provided the best habitat quality. Thatch depth, which has been suggested as an important cover component for *M. pennsylvanicus*, was significantly deeper at the southern site ($\bar{x} = 10.91 \pm 1.37$ cm) relative to the northern ($\bar{x} = 4.11 \pm 0.32$ cm) and central sites ($\bar{x} = 4.89 \pm 0.59$ cm, $F = 17.95$, $d.f. = 21$, $p < 0.001$, Duncan *post-hoc* test $p < 0.05$). In addition, the number of grass contacts observed at 10 cm off the ground was also significantly higher at the southern site ($\bar{x} = 84.2 \pm 9.25$ cm) relative to the northern ($\bar{x} = 27.25 \pm 6.64$ cm) and central sites ($\bar{x} = 38.75 \pm 4.45$ cm, $F = 18.21$, $d.f. = 57$, $p < 0.001$, Duncan *post-hoc* test $p < 0.05$).

DISCUSSION

Patterns in population size were quite different than what we had expected. Our naïve assumption had been that all aspects of population performance should be positively related to the amount of time since reclamation. Thus, we were expecting to observe the highest population sizes at the northern, as opposed to the southern, site. That population size was, if anything, highest at the southern site suggests that time since reclamation alone was a poor predictor of small mammal population performance in this system. Interestingly, studies of *Microtus pennsylvanicus* conducted in other, arguably less disturbed habitats (for example, old fields), have reported densities that, when adjusted for grid size differences, yield peak abundance estimates that range from 20.0–49.3 individuals for 40 × 40 m sampling areas (Yoder and others 1996; Dooley and Bowers 1998). Thus, our southern site exhibited population size responses that not only ex-

ceeded those observed at the other sites in our study, but also those observed in other, very different ecosystems.

That there was little evidence for population size differences during the winter months is to be expected. Once reproduction ceases in early autumn, *M. pennsylvanicus* populations generally quickly decline to extremely low numbers (for example, Dooley and Bowers 1998). The summer differences in population size more directly reflect the ability of these animals to respond to the habitat, particularly with local reproduction. That there was little statistical evidence for differences in survival between habitat patches is also not inconsistent with other studies of *M. pennsylvanicus* (Diffendorfer and others 1995, 1999; Dooley and Bowers 1998). Recruitment comparisons suggest but cannot unambiguously support the suggestion that populations at the southern study were increasing their numbers at a greater rate than at the other two sites. The overall test for differences in recruitment among sites was not significant; clearly there was a great deal of within-site variation. Arguably the most important demographic mechanism underlying increases in *M. pennsylvanicus* population size is local reproduction: each individual female has the capacity to produce close to 800 first- and second-generation descendants within one breeding season (Bowers, personal communication). Therefore the observation that the number of reproductive females was highest at the southern site suggests that by some measure the resource base there was stronger.

Results from our vegetation analysis would also appear to support the suggestion that habitat quality may have been substantially higher at the southern site relative to the northern and central sites and therefore could account, at least in part, for enhanced population size through the presence of a relatively higher number of reproductive females. Thatch depth and grass density (represented in our analyses as number of grass contacts), along with other aspects of habitat structure, have been associated with important variation in habitat quality for *M. pennsylvanicus* (Birney and others 1976; Getz 1985; Klatt and Getz 1987; Foster and Gaines 1991; Bowers and Dooley 1993). It is interesting to note that structural and biotic diversity appeared to be higher at the northern and central sites relative to the southern sites. Nonetheless, because *M. pennsylvanicus* is an obligate consumer of grasses, it may be that the relatively “newer” and less developed habitat afforded by the southern sites (that had only been recovering for about 15 years) provides the best quality habitat for this species. If so, it would be tempting to predict that population performance of *Microtus pennsylvanicus* should begin to resemble what was observed at the central and northern sites (both longer in the recovery process) as time progresses, and implicitly conclude that local succession, rather than landscape scale, effects will ultimately prove to be the most important drivers of small mammal demography. However, while the patterns reported here are consistent with such an interpretation, they do not definitively preclude alternative explanations. Local population fluctuations can occur in ways that seem largely

independent of local habitat quality (Krohne and others 1988). Emerging insights suggest that behavioral cues that are not yet fully explained hold the potential to play a large role in patch selection for many mammals (Swaigood, personal communication). In addition, there is a wealth of literature suggesting that demographic patterns may arise from responses to habitat variation operating simultaneously at a number of different scales (Bowers and others 1996; Pope and others 2000). In addition to this group of alternative hypotheses that simply represent notions drawn from contemporary population ecology, we should also add the possibility that the habitats we studied remain profoundly altered by the mining and reclamation processes and that such impacts may yet be exerting important influences on consumer population responses. Some literature has suggested that large-scale disturbances can lead to long-term and progressive degradations of plant-soil interactions thus yielding declining plant productivity. For example, Perry and others (1989) found that soils in a heavily disturbed ecosystem entered a "downward spiral in which deterioration with the soil resulted in further planting failures which in turn lead to further soil deterioration." Most recently, there seems to be a great deal of emphasis on the importance of re-establishing bacterial, ectomycorrhizal, and other soil biota in order to sustain long-term habitat health in restored ecosystems (Franklin and others 2000; Yin and others 2000). Even if soils are not deteriorating, it may be that legacy constraints may be delaying or preventing soil development and as such perpetuating the grassland stage of system development. Ironically, it might be the case that grassland species such as *Microtus pennsylvanicus* may in fact benefit. The delay or prevention of shrub and tree development might provide an unusually stable and therefore optimal habitat for consumers that would otherwise typically be forced from areas through the normal processes of successional development.

In order to distinguish between simple successional responses and the other alternative explanations that may account for the patterns observed here, we must determine whether the patterns we observed in this study vary over time or remain consistent. If simple successional responses fail to prove an adequate predictor of patterns in population performance, we may need to explore manipulative approaches such as soil transfer experiments (*sensu* Perry and others 1989) in order to test for effects of ongoing ecosystem degradation.

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